

SOME DISTASTEFUL ASIAN PAPILIONINAE (PAPILIONIDAE)

PETER SMETACEK

The Retreat, Jones Estate, Bhimtal, Nainital 263136, Uttaranchal, India, email: petersmetacek@rediffmail.com

ABSTRACT. Western Himalayan populations of three Asiatic *Papilio* L. species appear to be distasteful in varying degrees to birds. These include the polymorphic *Papilio polytes* L. which was considered a classic Batesian mimic of distasteful *Pachliopta* Reakirt. The Indian population of *polytes*, with three female forms, is a case of sympatric polymorphism in a distasteful species with warning coloration.

Additional key words: Müllerian mimicry; *Papilio*; polymorphic model

INTRODUCTION

Batesian mimicry, referring to a system comprising palatable species and unpalatable models, and Müllerian mimicry, involving similar-looking, unpalatable species, are well known examples of adaptive evolution by natural selection. Of the over 200 species of *Papilio* L. known, at least one W. African species (*antimachus* Drury) is known to be chemically protected in the adult stage (Watson & Whalley 1983). Several species are believed to be Batesian mimics of chemically defended moths and butterflies (Clarke & Sheppard 1960, 1962; Brower & Brower 1962; Clarke et al. 1968; Watson & Whalley 1983; etc.). Although the larvae of all *Papilio* butterflies are believed to be chemically protected by unpleasant taste and smell (Wynter-Blyth 1957; Klots & Klots 1959), this was not believed to be carried over to the adult stage except in the case of *antimachus*.

MATERIALS & METHODS

In a pilot study undertaken at Jones Estate, Bhimtal, in Nainital district, Uttaranchal, India (elevation 1500 m; latitude 29°20'41" N and longitude 79°36'15" E) in the outermost range of the Kumaon Himalaya, I presented >560 freshly collected, wild butterflies belonging to 86 species to wild, free ranging, foraging parties of birds in > 256 encounters over a period of 4 years (1999–2002). One or more of three *Papilio* species, i.e. *polyctor* Boisduval, *protenor* Cramer and *polytes* L. formed part of the presentation on 109 occasions. A total of 10 *polyctor* (9♂, 1♀), 9 *protenor* (8♂, 1♀) and 18 *polytes* (12♂, 6♀) were presented. Each specimen, if not devoured, was presented several times, sometimes on the same day, until it was too dry to be attractive to the birds.

The birds consisted of one family of White Crested Laughing Thrushes (*Garrulax leucolophus*), whose composition varied from 2 to 7 birds during the period of observation and White Throated Laughing Thrushes (*Garrulax albogularis*) in groups varying from 4 to >60 seasonally. Casual foraging species included Blue

Whistling Thrushes (*Myiophonus caeruleus*) and a Yellowcheeked Tit (*Parus xanthogenys*).

Laughing Thrushes are not known to attack butterflies on the wing. They feed on insects, berries and other vegetable matter (Ali 1962). White Crested and White Throated Laughing Thrushes spend most of their foraging time turning over dead leaves on the ground and investigating the bark and foliage of trees (Whistler 1935; Ali 1949).

They are very fond of live moths (*pers. obs.*). Initially the birds in this study were wary of dead butterflies but they soon developed a taste for them, especially control species belonging to Nymphalinae, of which 100% were eaten.

The lack of experience on the part of the birds and their evident willingness to learn proved advantageous, since they examined and tried to eat (at least once) every species presented, including known unpalatable species belonging to *Delias* Hübner, *Danaus* Latreille and *Pachliopta* Reakirt. White Crested Laughing Thrushes displayed a high degree of prey recognition at the species level. Many White Throated Laughing Thrushes ignored the butterflies completely throughout the study. The birds were observed from a distance of 3–4 m, initially through a wire mesh screen and later in the open.

RESULTS

Entire butterflies were offered, except on three different occasions when, after repeated rejections, the wing scales of 1 *polyctor* and 2 *protenor* specimens were wiped off and the wing shape altered to circumvent possible preconditioned visual aversion on the part of the birds. The *polyctor* was eaten but both the *protenor* continued to be ignored.

One ♂ 1 ♀ *polyctor*, 1 ♂ *protenor* and 4 ♂ 2 ♀ *polytes* were entirely eaten. The *protenor* was the only butterfly eaten by a Yellow-cheeked Tit on its single visit to the site. Ten percent of *polyctor*, 0% of *protenor* and 11.1% of *polytes* were partially eaten, usually the head and either thorax or abdomen. In all, 30% of *polyctor*,

11.1% of *protenor* and 44.4 % of *polytes* were entirely eaten, compared with 77% to 100% (mean 95%) for control species (*Colias fieldii* Ménétriés 77%; *Graphium sarpedon* Felder 90%; *Vanessa indica* Herbst 100%; *Kaniska canace* Linné 100%; *Symbrenthia lilaea* Hewitson 100% ; *Precis iphita* Cramer 100% ; *Junonia lemonias* Linné 100 % ; *Lethe roluria* Fabricius 90%; *Melanitis leda* Linné 100 % ; *Dendoryx epijarbas* Moore 95%) presented along with the *Papilio* species.

On one occasion, a White Crested Laughing Thrush that ate the abdomen and hindwings of a ♂ *polytes* and nothing else exhibited signs of distress immediately afterwards, opening its beak repeatedly as if to call but not emitting any sound. Such behavior was never observed in connection with the controls.

DISCUSSION

P. polyctor is not known to be mimetic, while *protenor* females have been proposed as Batesian mimics of the *Atrophaneura varuna* White group (Batwings) and three of the four female forms of the polymorphic *polytes* are considered classic Batesian mimics of *Pachliopta* (Evans 1932; Wynter-Blyth 1957; Clarke & Sheppard 1972; Larsen 1987). Peile (1937), quoting from T.R.D. Bell's series "Common Butterflies of the Plains of India" published in the *Journal of the Bombay Natural History Society*, stated that "the (*Pachliopta*) group is protected by very unpleasant smell and taste. Birds will not eat them nor will lizards willingly or readily. *P. polytes*, of a different group, is without these qualities ...". However, he did not qualify this statement further.

The male of *polytes* and one female form, *cyrus*, which occurs throughout the insect's range, are non-mimetic. The second female form, *romulus*, resembles

Pachliopta Hector L. and both are restricted to India and Sri Lanka. The nomino-typical form primarily resembles *Pachliopta aristolochiae* Fabricius and the two exhibit similar variation in wing pattern throughout their range from the Himalayas to Sri Lanka, Japan and Sulawesi. In addition, the typical form also resembles *Pachliopta polyphontes* Boisduval and *Pachliopta polydorus* L. in part of S.E. Asia. The form *theseus* of *polytes* resembles the black form of *aristolochiae* and both occur in parts of the Philippines and parts of Indonesia, while *Pachliopta atropos* Staudinger is a possible additional co-model on Palawan (Clarke & Sheppard 1972). In the present study, although three female forms of *polytes* occur in the area, only the *cyrus* form and males were used to preclude possible preconditioned visual aversion to the mimetic forms on the part of the birds. The possibility of significant differences in palatability between the female forms is unlikely, since all the forms in a given area (three in India and Sri Lanka) are obtainable from a single batch of eggs (Fryer 1913; Clarke & Sheppard 1972).

The above data strongly suggest that these three *Papilio* species are distasteful and that *polytes* is a Müllerian co-model rather a Batesian mimic of *Pachliopta*, at least in parts of its range. *P. polyctor* and *polytes* appear to be moderately distasteful while *protenor* is quite distasteful to birds at the study site (Table 1).

In the larval stage, these three species feed on members of the citrus family (Rutaceae). *P. polyctor* and *protenor* feed on *Xanthoxylum armatum* DC, while *polytes* feeds on a variety of rutaceous plants and has been bred on *Murraya königii* Spreng. and cultivated *Citrus* L. in the study area. Troidine swallowtails are known to sequester aristolochic acids from their

TABLE 1. Pooled responses of White Crested and White Throated Laughing Thrushes to freshly collected, wild, dead butterflies. Butterflies that were manipulated for +5 seconds by one or more birds and then rejected are recorded in column 6. The response score (column 7) was calculated from scores recorded for individual presentations: 0 = ignored, flung aside, pecked briefly or repeatedly but not eaten (this information was recorded in words); 1= the butterfly was partially eaten, usually the head and either thorax or abdomen (specimens preserved in my collection) and 2 = the entire body, but not necessarily the wings, was eaten. Specimens were collected at the study site in Jones Estate and at Ranibagh (altitude 600 m), 20 km. south by road from Jones Estate, mainly in March–April and October–November.

1 Species	2 Specimens Presented	3 # of encounters	4 # entirely eaten		5 # partially eaten		6 # of times rejected	7 Response Score			
			Specimens	%	Specimens	%		% of encounters	Max possible	Actual	%
Control	123	133	117	95.1	3	2.4	3	2.2	246	238	95.9
<i>polyctor</i>	10	33	2	20	2	20	4	12	20	6	30
<i>protenor</i>	9	32	1	11	0	0	4	12.5	18	2	11.1
<i>polytes</i>	18	49	6	33	4	22	7	14	36	16	44.4

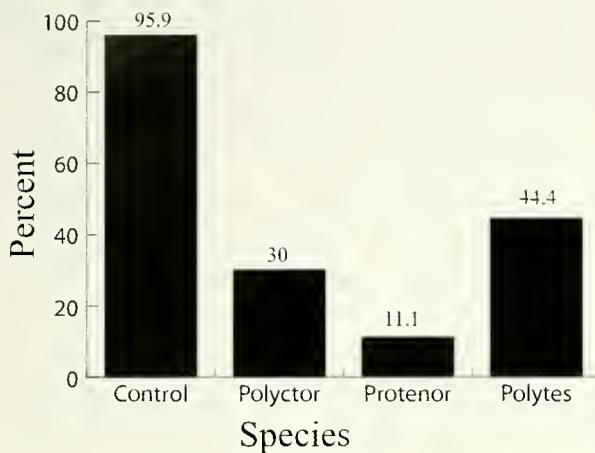


FIGURE 1. Palatability index for the percentage of butterflies entirely or partially eaten by wild birds, based on response score described in Table 1. Butterflies were presented randomly.

hostplants (Brown *et al.* 1991) and it is possible that some *Papilio* butterflies, such as the species considered in this paper, have retained the ability to sequester aromatic or distasteful compounds from their larval hostplants. Although some *Papilio* species are known to be palatable to birds, such as the N. American *glaucus* L. and *palamades* Drury, which have been used as controls (95% eaten) in another study (Ritland & Brower 1991), both species do not feed on Rutaceae but on Rosaceae, Oleaceae, Salicaceae, Betulaceae, Lauraceae and Magnoliaceae (Scriber *et al.* 1975; Watson & Whalley 1983; Daccordi *et al.* 1988). In the present study, *Graphium* Scopoli species that feed on Lauraceae were found to be attractively palatable to the birds (unpublished) and one was used as a control.

In this study, the spring and summer broods of *polycitor*, the spring brood of *protenor* and spring and autumn broods of *polytes* were used. The results do not suggest any noticeable difference in distastefulness between the broods.

The present study was carried out using wild, free-ranging birds which are not habitual predators on butterflies but generalized insectivores. The study involved the random presentation of wild butterflies. The birds could be observed only while they were at the study site. Since they usually departed soon after eating, possible distress behavior or even regurgitation could not always be observed. Rigorous measurements of manipulation time, number of times pecked and other minutiae were not always possible in the mêlée caused by a large number of birds feeding on a small patch of ground. The birds at times arrived and devoured everything in sight and at other times ignored everything, including controls, having evidently found sufficient food elsewhere.

Although extrapolation of the results obtained from the small number of *Papilio* specimens offered in this study must be done with caution, there is little doubt that at least some populations of the three *Papilio* species are distasteful in varying degrees to some birds.

The present findings prompt a re-interpretation of the relationship between *polytes* and *Pachliopta*. The classic Batesian interpretation of *polytes*-*Pachliopta* mimicry predicted that only *polytes* benefits at the expense of *Pachliopta*, which it "parasitises", and predators, which it deceives into shunning palatable prey. The new Müllerian interpretation suggests that the shared aposematic signals of the co-models (*polytes* and *Pachliopta* spp.) result in enhanced predator learning and the benefits of this accrue to all the butterfly species involved. The relationship between the butterflies is one of asymmetrical Müllerian mimicry, since *polytes* appears to be only moderately distasteful while the *Pachliopta* genus is certainly more distasteful, with aristolochic acids in the body tissue.

The distastefulness of *polytes* also explains the persistence of the non-mimetic female form *cyrus* over the entire range of the species. Although *cyrus* comprises only 5% of the total female population in parts of southern India where *aristolochiac*, *hector* and the corresponding female forms of *polytes* are very common (Larsen 1987), it predominates in the western Himalayan foothills where *hector* is absent and *aristolochiae* scarce or absent (Peile 1937; Wynter-Blyth 1957) but where *polytes* is as common as in other parts of its range. Indeed, the presence or absence of its co-models hardly affects the abundance of *polytes* over its range, as in the Himalayan foothills of Himachal Pradesh, India, where it is not uncommon despite the fact that none of its co-models occur (DeRhe-Philippe 1931).

Polymorphism in distasteful species with warning coloration is an unusual phenomenon (Joron & Mallet 1998; Kapan 2001), since genetic analysis of Müllerian mimicry indicated that selection is for monomorphism rather than polymorphism (Turner & Crane 1962; Sheppard 1963; Emsley 1964). In other known polymorphic Müllerian co-models, such as *Heliconius cydno* Doubleday & Hewitson and *Heliconius erato* L., different forms of the same species are rarely sympatric (Joron & Mallet 1998). In the very likely event that all populations of *polytes* are as distasteful as the western Himalayan one, the case of *polytes* in southern India is unusual, since the two mimetic forms of the female which occur there are roughly equally abundant (Peile 1937), eg. *hector*-like form 50.4% and *aristolochiae*-like form 45.7% at a single location (Larsen 1987).

It has been proposed (Kapan 2001) that geographical

variation in selection for mimicry coupled with weak selection against forms when they are common explains the existence of polymorphic Müllerian co-models. Although this proposition is applicable to certain cases, notably *Heliconius Kluk*, it cannot be applied to the case of sympatric polymorphism in *polytes* in southern India.

ACKNOWLEDGEMENTS

This work would have been impossible without the help of wife, Rajani Smetacek, who gained the confidence of the birds over many years and undertook some of the observations when I was not at home.

LITERATURE CITED

- ACKERY, P.R. & R.I. VANE-WRIGHT. 1984. Milkweed butterflies—their cladistics and biology. Brit. Mus. (N.H.). London. 425 pp.
- ALI, S. 1949. Indian Hill Birds. Oxford Univ. Press, Delhi. 42+426 pp.
- . 1962. The Birds of Sikkim. Oxford Univ. Press, Delhi. 30+414 pp; 26 pl.
- BROWER, L.P. & J. VAN Z. BROWER. 1962. The relative abundance of model and mimic butterflies in natural populations of the *Battus philenor* mimicry complex. Ecology 43: 154–158.
- BROWN, K.S. JR., J.R. TRIGO, R.B. FRANCINI, A.B. BARROS DE MORAIS & P.C. MOTTA. 1991. In Plant-Animal Interactions (eds. Price, P.W., T.M. Lewinsohn, G.W. Fernandes & W.W. Benson). Wiley, New York. 375–402 pp. quoted by Vane-Wright, R.I. 1991. A case of self-deception. Nature, London. 350: 460–461.
- CLARKE, C.A. & P.M. SHEPPARD. 1960. The evolution of mimicry in the butterfly *Papilio dardanus*. Heredity 14: 163–173.
- . 1962. The genetics of the mimetic butterfly *Papilio glaucus*. Ecology 43: 159–161.
- CLARKE, C.A. & P.M. SHEPPARD & I.W.B. THORNTON. 1965. The genetics of the mimetic butterfly *Papilio memnon* L.. Phil. Trans. R. Soc. Lond. B 254: 37–89.
- CLARKE, C.A. & P.M. SHEPPARD. 1972. The genetics of the mimetic butterfly *Papilio polytes* L.. Phil. Trans. R. Soc. Lond. B 263: 431–455.
- DACCORDI, M., P. TRIBERTI & A. ZANETTI. 1955. The Macdonald Encyclopedia of Butterflies and Moths. Macdonald, London. pp. 353.
- DERHIÉ-PHILIPPE, G.W.V. 1931. The butterflies of the Simla Hills. J. Bomb. Nat. Hist. Soc. 35: 172–183.
- EMSLEY, M. G. 1964. The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationship between the two species. Zoologica 49: 245–256.
- EVANS, W.H. 1932. The Identification of Indian Butterflies. 2nd ed., Bombay Nat. Hist. Soc. 10+454 pp.
- FRYER, J.C.F. 1913. An investigation by pedigree breeding into the polymorphism of *Papilio polytes*, Linn.. Phil. Trans. R. Soc. Lond. B. 204: 227–254.
- JORON, M. & J.L. MALLET. 1995. Diversity in mimicry: paradox or paradigm. Trends Ecol. Evol. 13: 461–466.
- KAPAN, D.D. 2001. Three butterfly system provides a field test of Müllerian mimicry. Nature, London, 409: 335–340.
- KLOTS, A.B. & E.B. KLOTS. 1959. Living Insects of the World. Hamish Hamilton, London. 304 pp.
- LARSEN, T.B. 1957. The butterflies of the Nilgiri mountains of Southern India. J. Bombay Nat. Hist. Soc. 54: 26–54.
- PEILE, H. D. 1937. A Guide to Collecting Butterflies of India. Staples, London. 14+312 pp.
- RITLAND, D.B. & L.P. BROWER. 1991. The viceroy butterfly is not a Batesian mimic. Nature, London 350: 497–498.
- SCRIBER, J.M., R.C. LEDERHOUSE & L. CONTARDO. 1975. Spicebush, *Lindera benzoin*, a little known food plant of *Papilio glaucus* (Papilionidae). J. Lep. Soc. 29: 10–14.
- SHEPPARD, P.M. 1963. Some genetic studies of Mullerian mimics in butterflies of the genus *Heliconius*. Zoologica 45: 145–154.
- TURNER, J.R.G. & J. CRANE. 1962. The genetics of some polymorphic forms of the butterflies *Heliconius melpomene* Linnaeus and *Heliconius erato* Linnaeus. 1. Major genes. Zoologica 47: 141–152.
- WATSON, A., P.E.S. WHALLEY & W.D. DUCKWORTH. 1983. The Dictionary of Butterflies and Moths in Color. Peering, London. 14+296 pp.
- WHISTLER, H. 1935. Popular Handbook of Indian Birds. Gurney & Jackson, London. pp 25–30.
- WINTER-BLYTH, M.A. 1957. Butterflies of the Indian Region. Bombay Natural History Society, Bombay. 20+523 pp.

Received 15 November 2004; revised and accepted 23 December 2005